

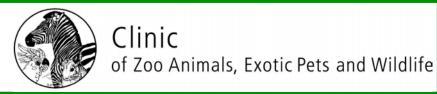
# Low energy requirements in an artiodactyl family: the case of the camelids



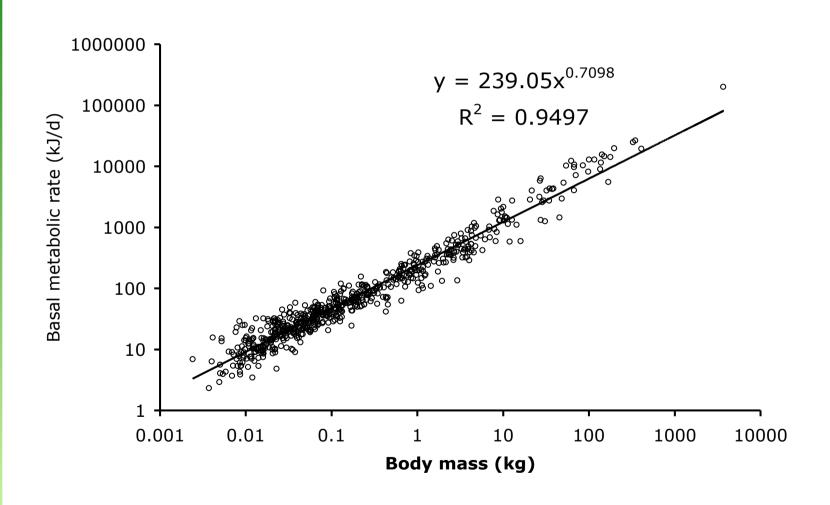
M.T. Dittmann<sup>1,2</sup>, J. Hummel<sup>3</sup>, U. Runge<sup>4</sup>, C. Galeffi<sup>5</sup>, M. Clauss<sup>1</sup>

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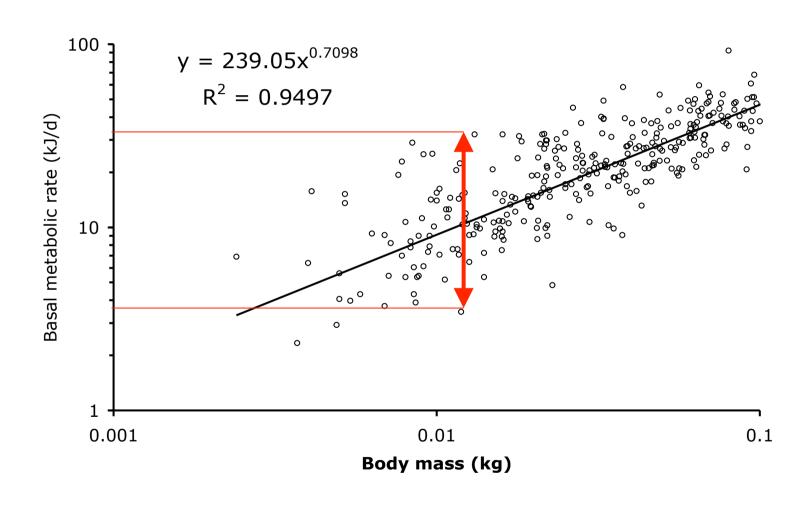














Reasons for systematic variation in the level of mammalian metabolism:

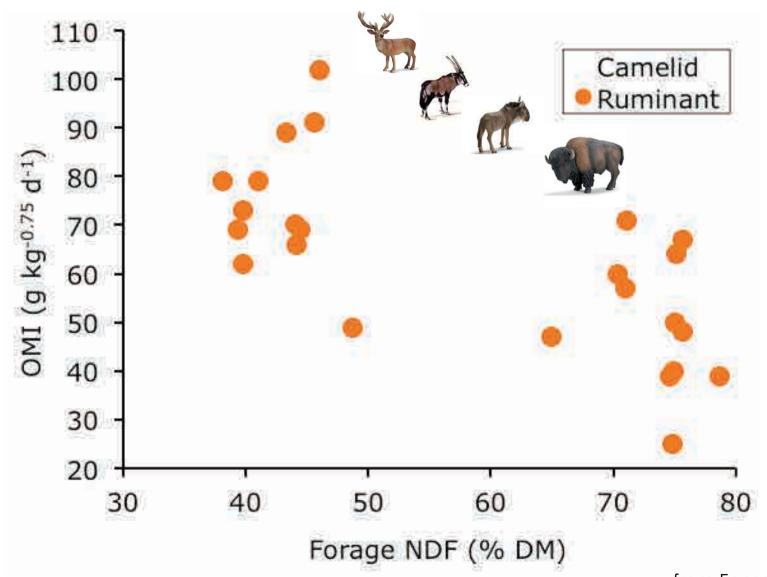
- habitat
  - arctic vs. tropic
  - marine vs. terrestrial
  - ground vs. subterranean



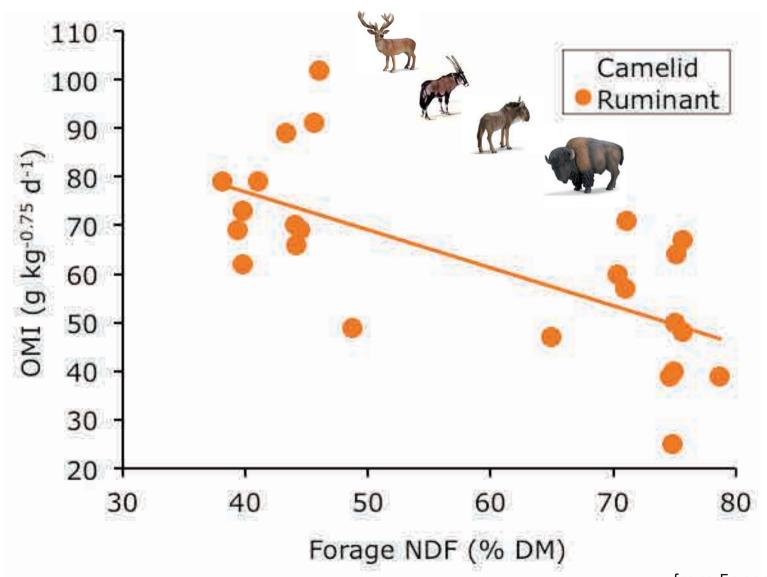
Reasons for systematic variation in the level of mammalian metabolism:

- habitat
  - arctic vs. tropic
  - marine vs. terrestrial
  - ground vs. subterranean
- phylogeny
  - marsupials vs. eutheria
  - xenarthra vs. other eutheria
  - camelids ? (vs. ruminants)

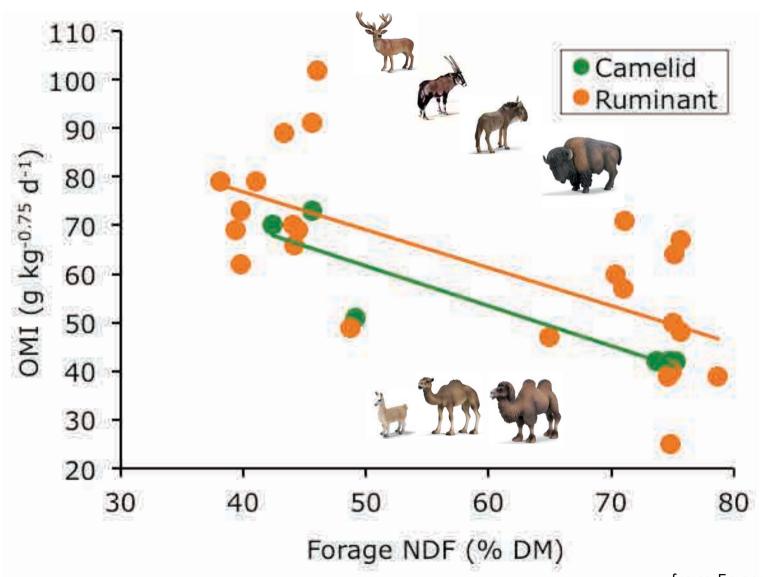




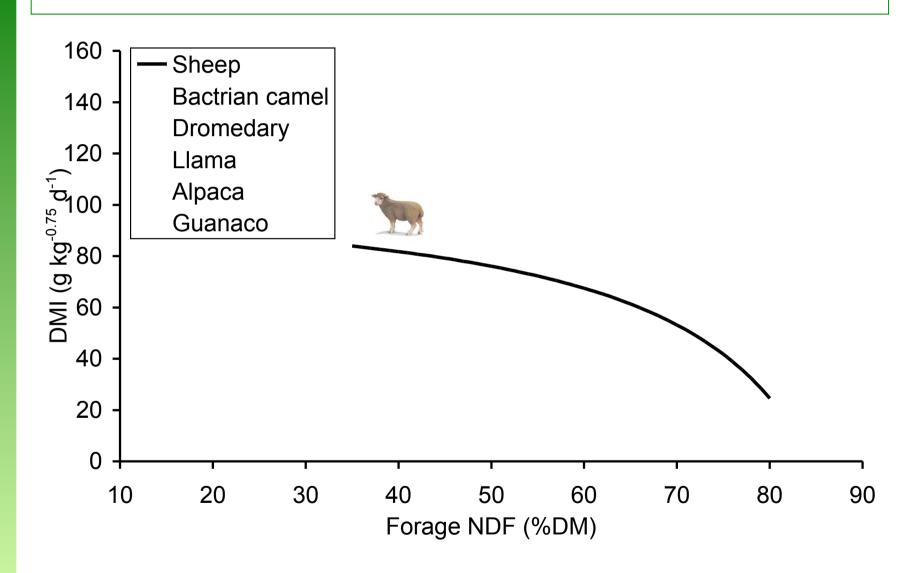




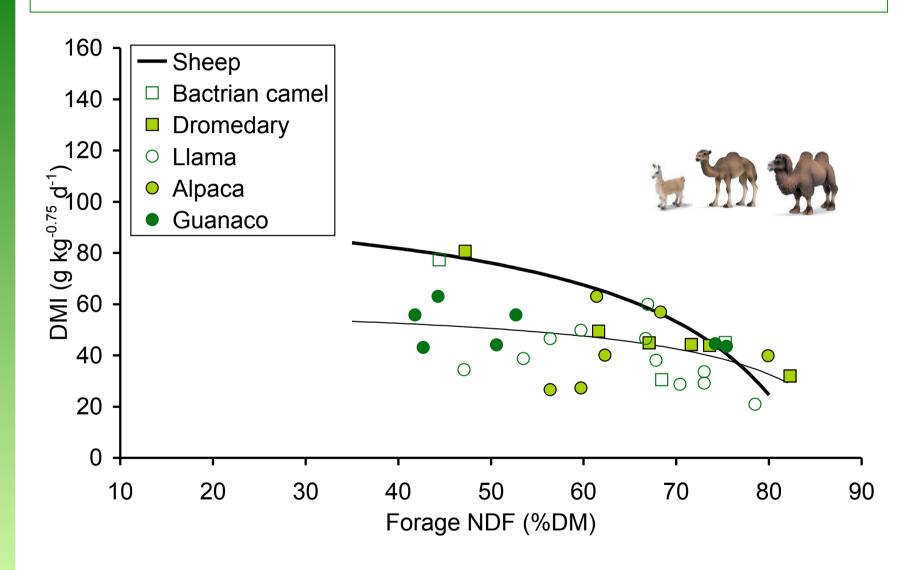






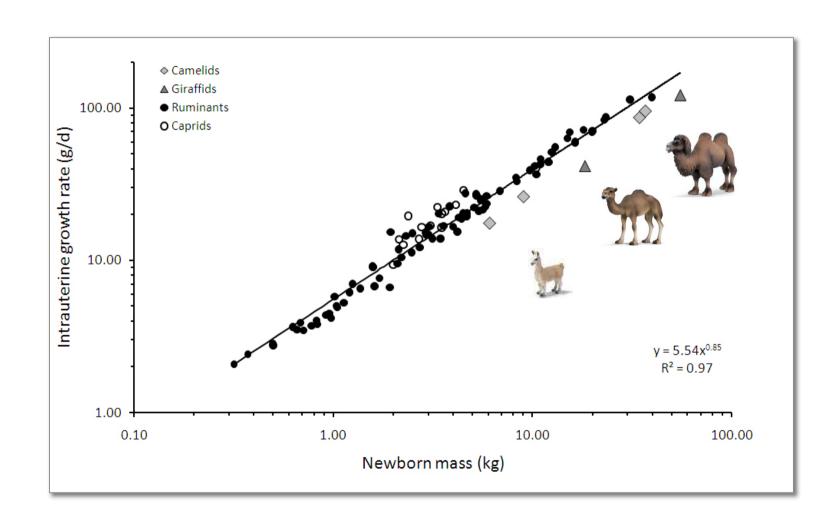








### Presumptive evidence II: life history





#### Presumptive evidence III: fossil sequence

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#### MODELLING EQUID/RUMINANT COMPETITION IN THE FOSSIL RECORD

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(Received November 2, 1993)

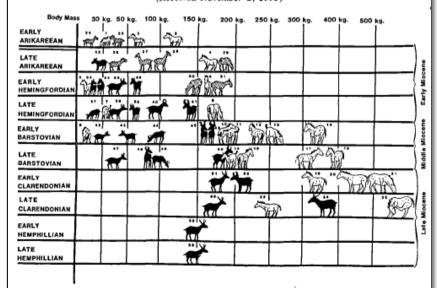
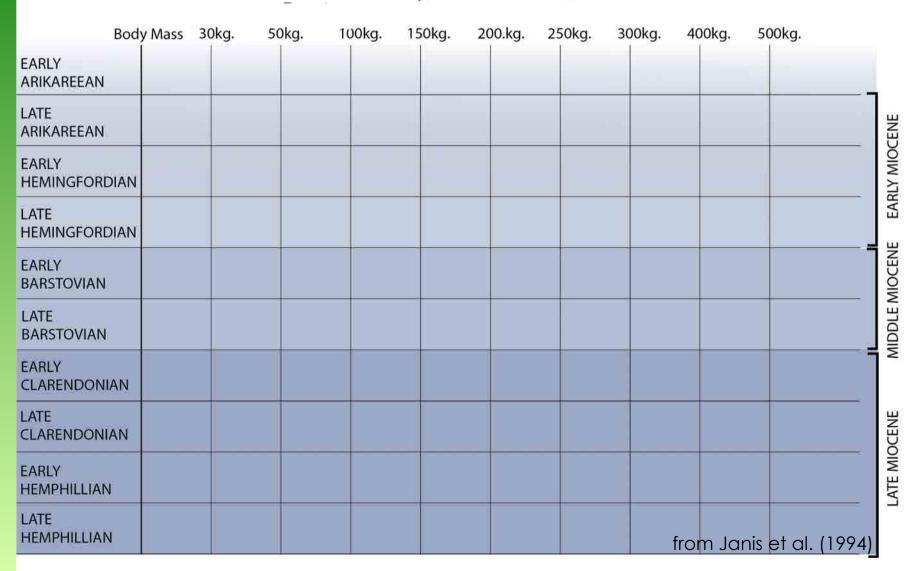


Figure 3 Body size distribution of browsing Miocene equids and ruminants. Key to ungulate taxa:

A. Color of taxon: Striped horses=Mesohippines; white horses=Anchitherines; spotted horses=Hypohippines; black artiodactyls=Pecorans; cross-hatched artiodactyls=Tylopods.

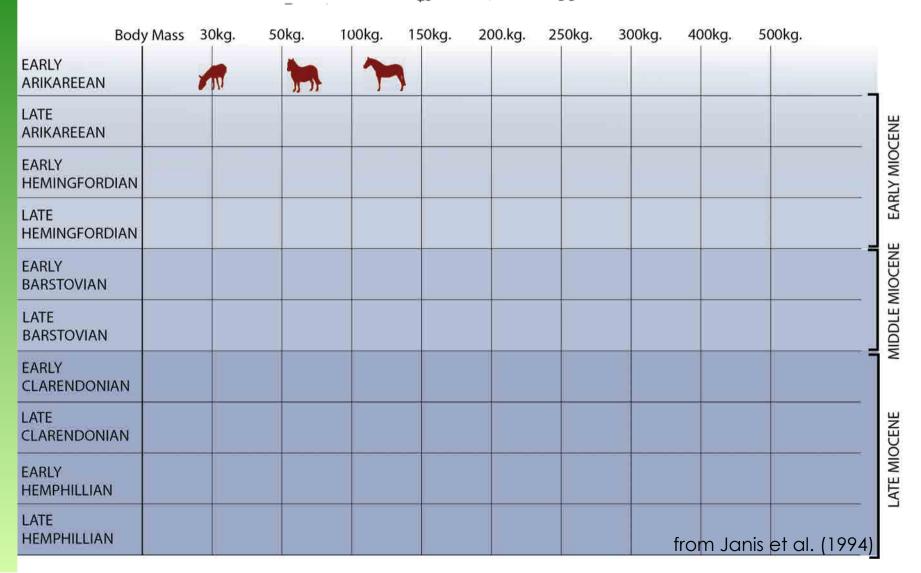


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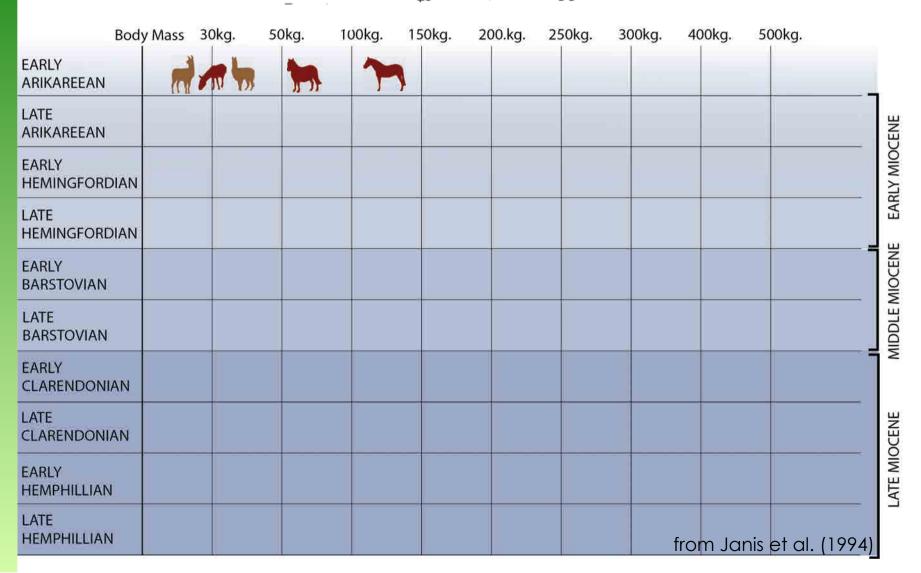


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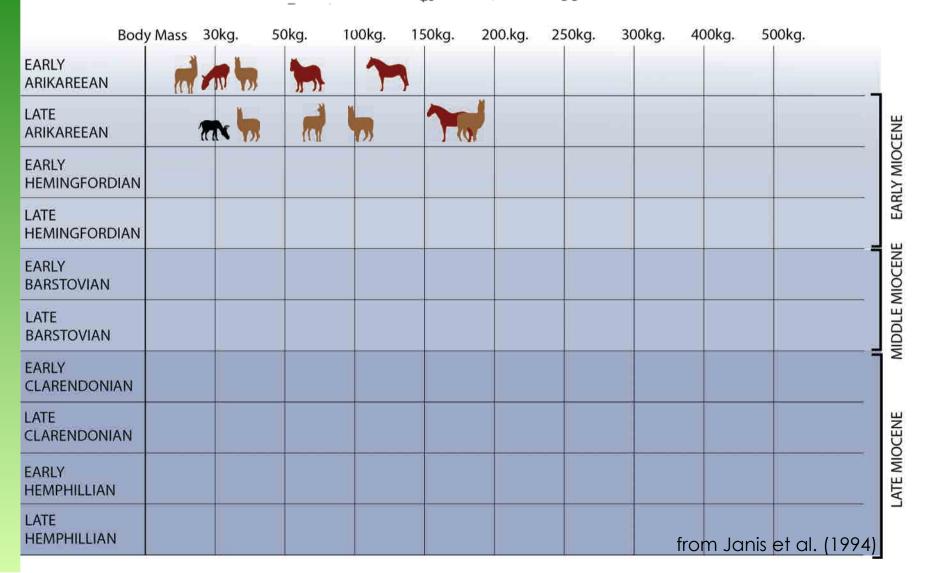


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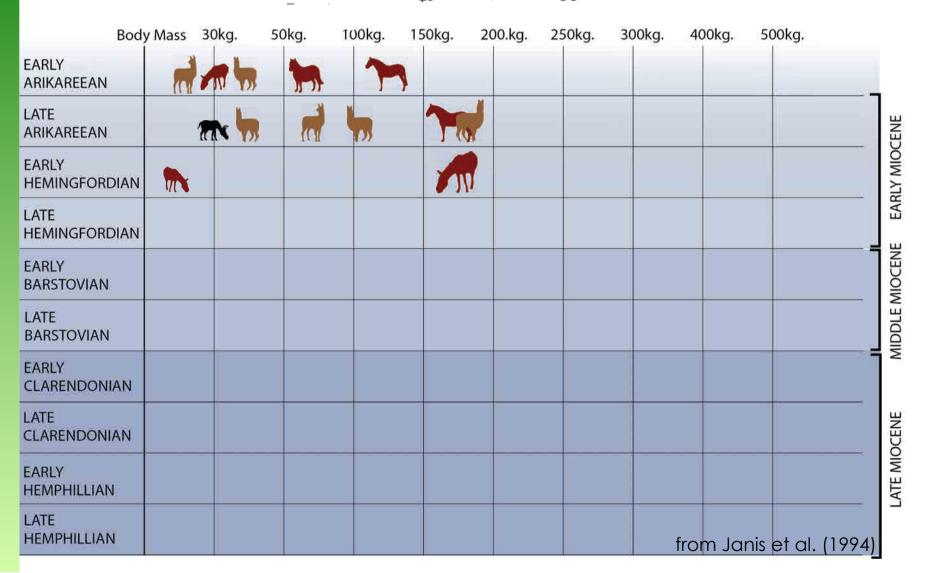


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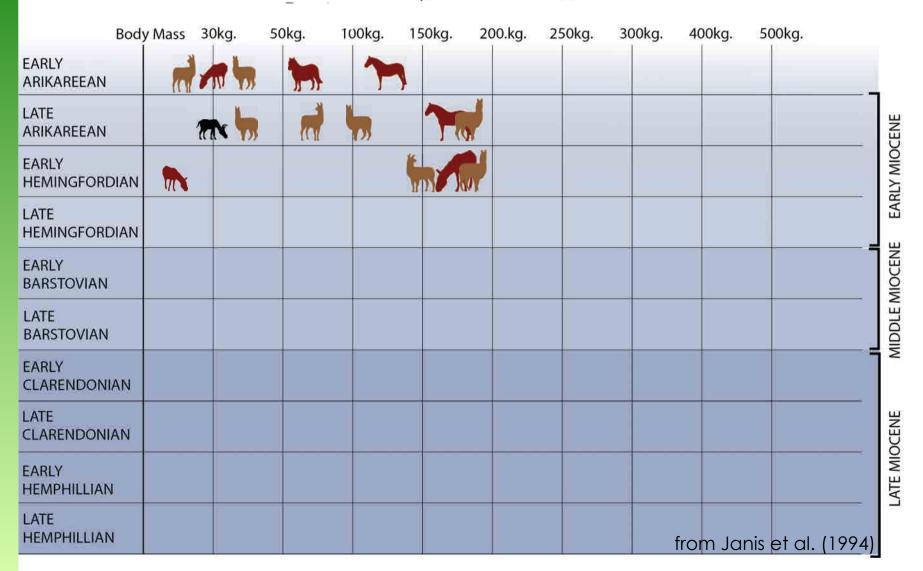


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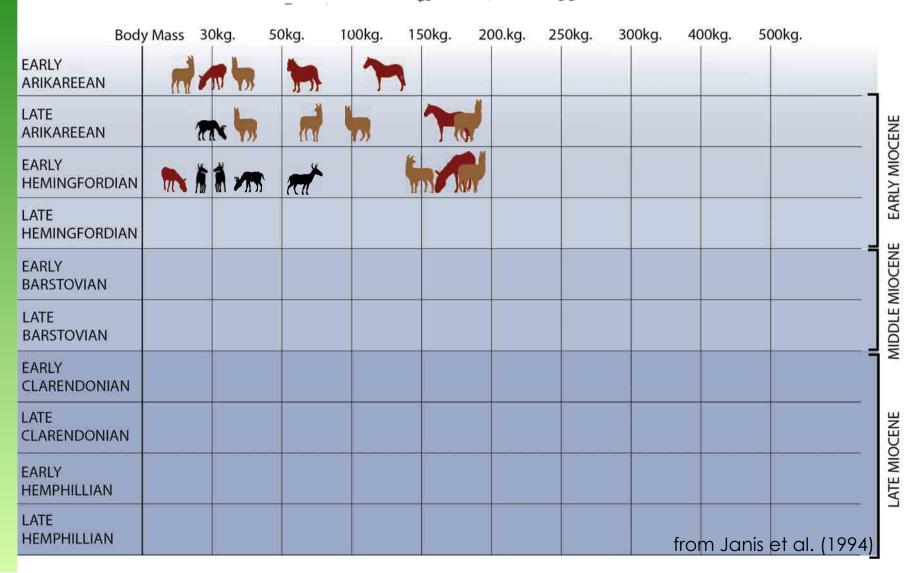


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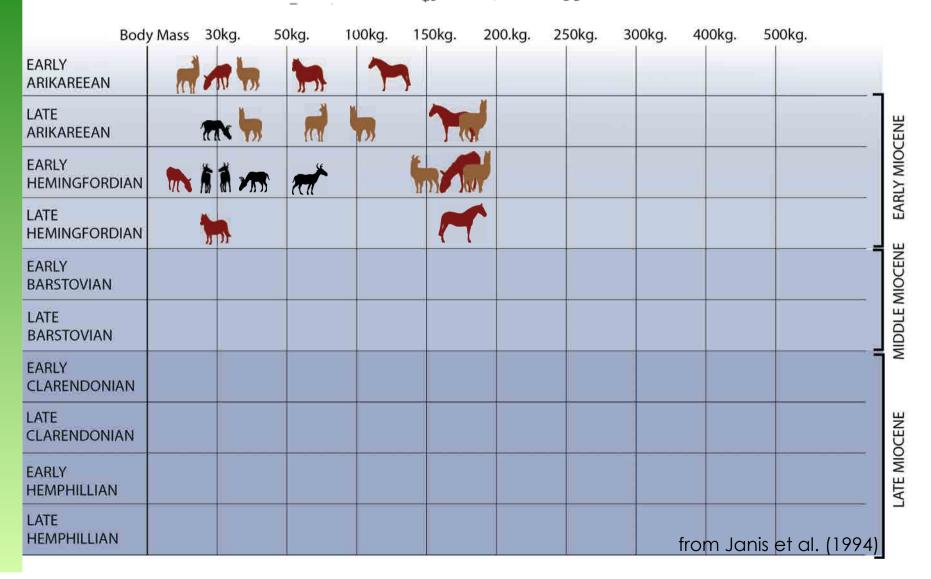


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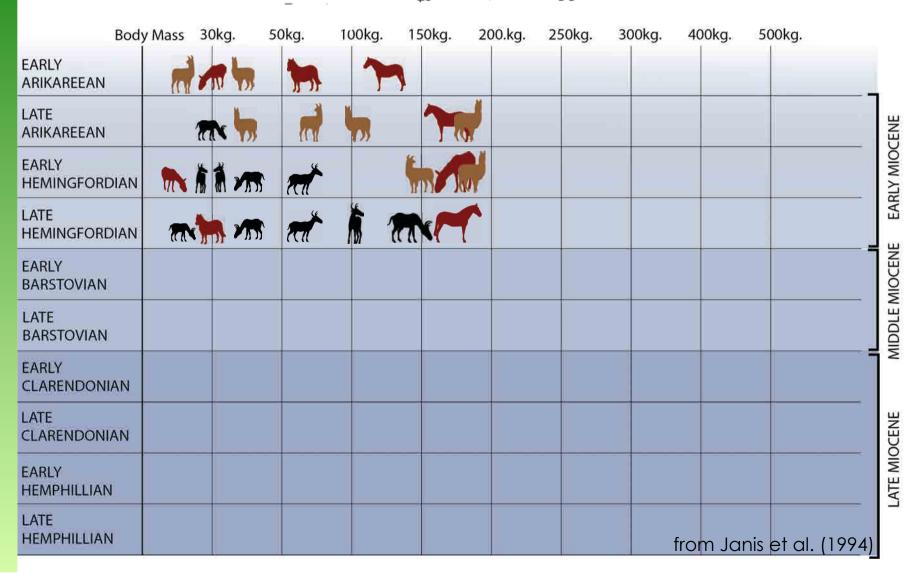


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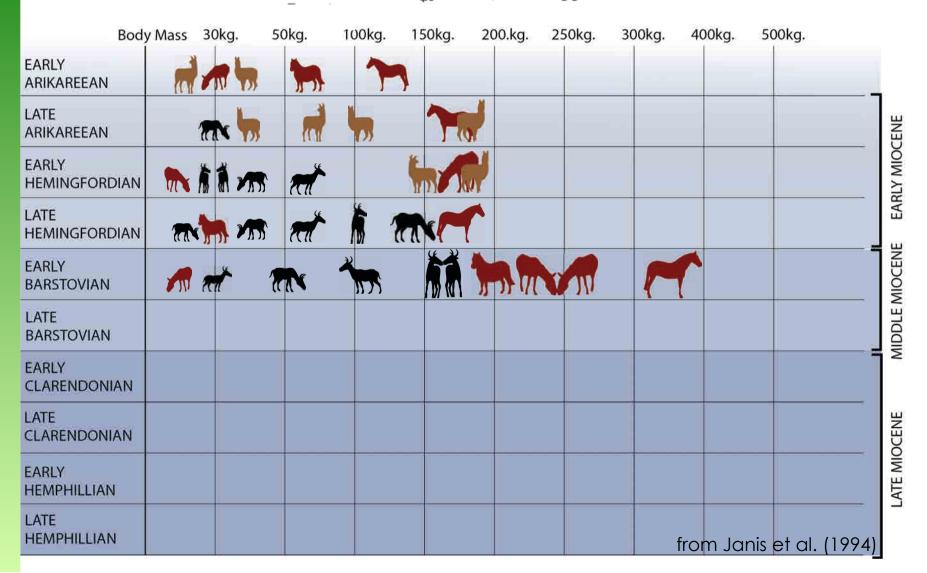


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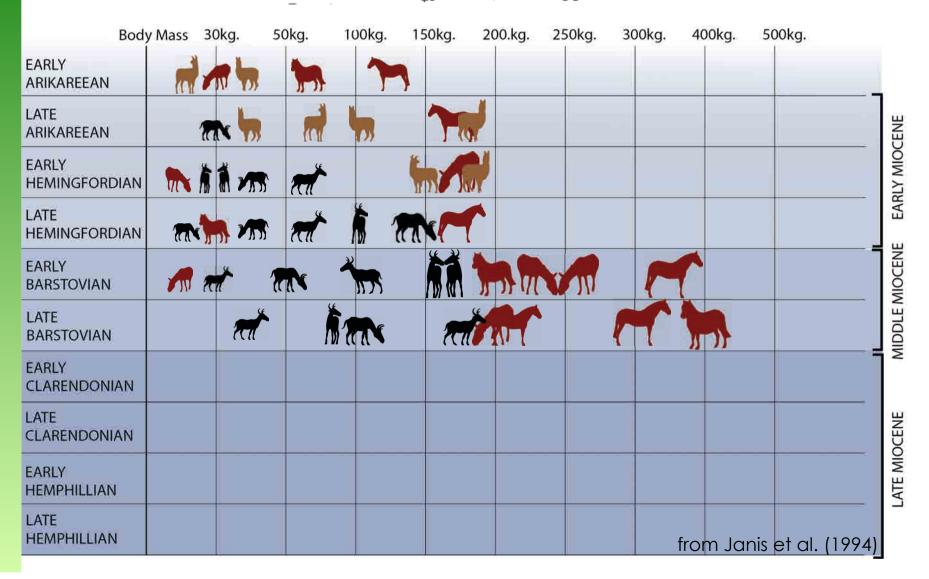


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### Question

Does more concrete evidence exist that camelids, as a taxonomic group, are characterised by a low level of metabolism?



#### Methods

- 1. Literature data: comparative food intake in camelids and domestic ruminants
  - a) ad libitum food access
  - b) roughage-only diets
  - c) only studies that compared at least one camelid and one ruminant species in the same experiment



#### Methods

- 1. Literature data: comparative food intake in camelids and domestic ruminants
  - a) ad libitum food access
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- 2. Oxygen consumption (chamber respirometry) in alpacas, llamas and Bactrian camels



18 publications, 75 direct comparisons

Comparisons on the basis of kg<sup>0.75</sup> kg<sup>0.9</sup>

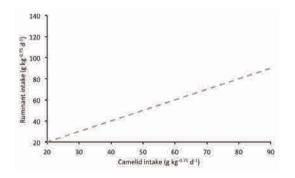
kg<sup>1.0</sup>

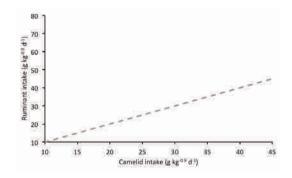


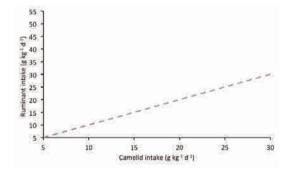
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kg<sup>1.0</sup>





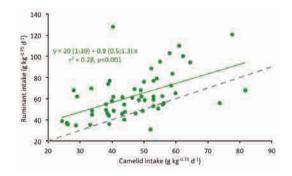


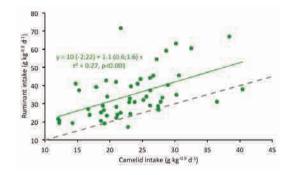


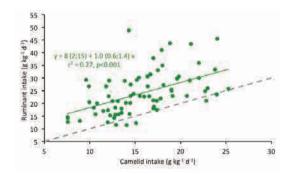
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kg<sup>1.0</sup>





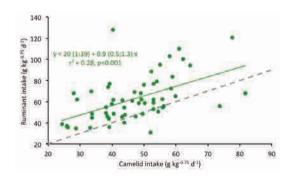


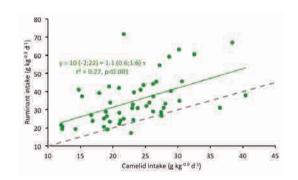


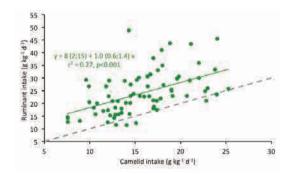
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Comparisons on the basis of kg<sup>0.75</sup> kg<sup>0.9</sup>

kg1.0







Ruminant intake higher by a factor of  $1.4 \pm 0.4$   $1.5 \pm 0.5$ 

 $1.6 \pm 0.5$ 























5 alpacas, 6 llamas, 5 Bactrian camels

constant access to food (lucerne) and water measurements in winter

Portable pumps and analyser (Turbofox, Sable Systems)

O<sub>2</sub> x 20.08 J/L all data = (maintenance) metabolic rate 20 lowest data points = resting metabolic rate



| Requirement | Species | Value  | Reference              |
|-------------|---------|--|------------------------|
| MEm         | Goat    | 423-576 kJ kg <sup>-0.75</sup> d <sup>-1</sup> | (GfE, 2003; NRC, 2007) |
|             | Sheep   | 390-447 kJ kg <sup>-0.75</sup> d <sup>-1</sup> | (GfE, 1996; NRC, 2007) |
|             | Cattle  | 488-537 kJ kg <sup>-0.75</sup> d <sup>-1</sup> | (GfE, 1995)            |



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| Species                             | MEm                | MR | Standing<br>MR             | Resting<br>MR   | Fasting<br>MR | Source  | Based on  |
|-------------------------------------|--------------------|----|----------------------------|-----------------|---------------|---|---|
|                                     |                    |    | kJ kg <sup>-0.75</sup> day | y <sup>-1</sup> |               |   |   |
| SAC                                 | 305                |    |                            |                 |               | (Van Saun, 2006; NRC, 2007)   | Literature data   |
| Alpaca<br>Alpaca<br>Alpaca          | 297<br>276<br>440  |    |                            |                 |               | (Flores et al., 1989)<br>(Newman and Paterson, 1994)<br>(Russel and Redden, 1997)                     | Cited in: (López and Raggi, 1992; San Martín, 1996)<br>Intake & BM change<br>Intake & BM change |
| Llama<br>Llama                      | 256                |    |                            |                 |               | (Schneider et al., 1974; Rübsamen<br>and von Engelhardt, 1975; von<br>Engelhardt and Schneider, 1977) | Intake & BM change, chamber respirometry  |
| Llama<br>Llama<br>Llama<br>Llama    | 310-354<br>296-343 |    |                            |                 |               | (Carmean et al., 1992)<br>(Vernet et al., 1997)   | Chamber respirometry & heat production<br>Chamber respirometry & heat production                |
| Dromedary<br>Dromedary<br>Dromedary |                    |    |                            |                 |               |   |   |
| Dromedary<br>Dromedary              | 359                |    |                            |                 |               | (Farid et al., 1990)  | Intake & BM change  |
| Dromedary<br>Dromedary<br>Dromedary | 374<br>304         |    |                            |                 |               | (Farid, 1995)<br>(Guerouali et al., 1995)   | Intake & BM change<br>Chamber respirometry & heat production                                    |





| Species   | MEm                | MR         | Standing<br>MR             | Resting<br>MR            | Fasting<br>MR | Source  | Based on   |
|---|--------------------|------------|----------------------------|--------------------------|---------------|---|--|
|   |                    |            | kJ kg <sup>-0.75</sup> day | / <sup>-1</sup>          |               |   |  |
| SAC   | 305                |            |                            |                          |               | (Van Saun, 2006; NRC, 2007)   | Literature data  |
| Alpaca<br>Alpaca<br>Alpaca  | 297<br>276<br>440  |            |                            |                          |               | (Flores et al., 1989)<br>(Newman and Paterson, 1994)<br>(Russel and Redden, 1997)   | Cited in: (López and Raggi, 1992; San Martín, 1996)<br>Intake & BM change<br>Intake & BM change  |
| Llama   | 256                |            |                            |                          | 218           | (Schneider et al., 1974; Rübsamen<br>and von Engelhardt, 1975; von<br>Engelhardt and Schneider, 1977)   | Intake & BM change, chamber respirometry   |
| Llama<br>Llama<br>Llama<br>Llama<br>Llama                                       | 310-354<br>296-343 | 313<br>290 | 363<br>341                 |                          | 248           | (El-Nouty et al., 1978)<br>(Hochachka et al., 1987)<br>(Carmean et al., 1992)<br>(Vernet et al., 1997)<br>(Nielsen et al., 2010)  | Mask respirometry Mask respirometry Chamber respirometry & heat production Chamber respirometry & heat production Chamber respirometry                                 |
| Dromedary Dromedary Dromedary Dromedary Dromedary Dromedary Dromedary Dromedary | 359<br>374<br>304  |            | 256<br>216<br>299          | 215<br>206<br>230<br>203 | 213           | (Schmidt-Nielsen et al., 1967)<br>(Schmidt-Nielsen et al., 1981)<br>(Yousef et al., 1989)<br>(Farid et al., 1990)<br>(Evans et al., 1994)<br>(Farid, 1995)<br>(Guerouali et al., 1995)<br>(Maloiy et al., 2009) | Mask respirometry Mask respirometry Mask respirometry Intake & BM change Mask respirometry Intake & BM change Chamber respirometry & heat production Mask respirometry |





| Species        | MEm                | MR  | Standing<br>MR             | Resting<br>MR | Fasting<br>MR                           | Source  | Based on   |
|----------------|--------------------|-----|----------------------------|---------------|---|---|--|
|                | e e                |     | kJ kg <sup>-0.75</sup> day | /-1           | *************************************** | <del>.</del>  |  |
| SAC            | 305                |     |                            |               |   | (Van Saun, 2006; NRC, 2007)   | Literature data  |
| Alpaca         | 297                |     |                            |               |   | (Flores et al., 1989)   | Cited in: (López and Raggi, 1992; San Martín, 1996)                              |
| Alpaca         | 276                |     |                            |               |   | (Newman and Paterson, 1994)   | Intake & BM change   |
| Alpaca         | 440                |     |                            |               |   | (Russel and Redden, 1997)   | Intake & BM change   |
| Alpaca         |                    | 215 |                            | 144           |   | this study  | Chamber respirometry   |
| Llama          | 256                |     |                            |               | 218                                     | (Schneider et al., 1974; Rübsamen<br>and von Engelhardt, 1975; von<br>Engelhardt and Schneider, 1977) | Intake & BM change, chamber respirometry   |
| Llama<br>Llama |                    |     | 363<br>341                 |               |   | (El-Nouty et al., 1978)<br>(Hochachka et al., 1987)   | Mask respirometry Mask respirometry  |
| Llama<br>Llama | 310-354<br>296-343 | 313 |                            |               | 248                                     | (Carmean et al., 1992)<br>(Vernet et al., 1997)   | Chamber respirometry & heat production<br>Chamber respirometry & heat production |
| Llama          |                    | 290 |                            |               |   | (Nielsen et al., 2010)  | Chamber respirometry   |
| Dromedary      |                    |     |                            | 215           |   | (Schmidt-Nielsen et al., 1967)  | Mask respirometry  |
| Dromedary      |                    |     |                            | 206           |   | (Schmidt-Nielsen et al., 1981)  | Mask respirometry  |
| Dromedary      |                    |     | 256                        | 230           |   | (Yousef et al., 1989)   | Mask respirometry  |
| Dromedary      | 359                |     |                            |               |   | (Farid et al., 1990)  | Intake & BM change   |
| Dromedary      |                    |     | 216                        | 203           |   | (Evans et al., 1994)  | Mask respirometry  |
| Dromedary      | 374                |     |                            |               |   | (Farid, 1995)   | Intake & BM change   |
| Dromedary      | 304                |     |                            |               | 213                                     | (Guerouali et al., 1995)  | Chamber respirometry & heat production   |
| Dromedary      |                    |     | 299                        |               |   | (Maloiy et al., 2009)   | Mask respirometry  |





| Species                             | MEm                                     | MR  | Standing<br>MR             | Resting<br>MR     | Fasting<br>MR | Source  | Based on  |
|-------------------------------------|---|-----|----------------------------|-------------------|---------------|---|---|
|                                     | 8                                       |     | kJ kg <sup>-0.75</sup> day | 7-1               |               | •   |   |
| SAC                                 | 305                                     |     |                            |                   |               | (Van Saun, 2006; NRC, 2007)   | Literature data                                       |
| Alpaca                              | 297                                     |     |                            |                   |               | (Flores et al., 1989)   | Cited in: (López and Raggi, 1992; San Martín, 1996)   |
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| Alpaca                              | *************************************** | 215 |                            | 144               |               | this study  | Chamber respirometry                                  |
| Llama                               | 256                                     |     |                            |                   | 218           | (Schneider et al., 1974; Rübsamen<br>and von Engelhardt, 1975; von<br>Engelhardt and Schneider, 1977) | Intake & BM change, chamber respirometry              |
| Llama                               |   |     | 363                        |                   |               | (El-Nouty et al., 1978)   | Mask respirometry                                     |
| Llama                               |   |     | 341                        |                   |               | (Hochachka et al., 1987)  | Mask respirometry                                     |
| Llama                               | 310-354                                 |     |                            |                   | 248           | (Carmean et al., 1992)  | Chamber respirometry & heat production                |
| Llama                               | 296-343                                 | 313 |                            |                   |               | (Vernet et al., 1997)   | Chamber respirometry & heat production                |
| Llama                               |   | 290 |                            |                   |               | (Nielsen et al., 2010)  | Chamber respirometry                                  |
| Llama                               |   | 261 |                            | 164               |               | this study  | Chamber respirometry                                  |
| Dromedary<br>Dromedary<br>Dromedary |   |     | 256                        | 215<br>206<br>230 |               | (Schmidt-Nielsen et al., 1967)<br>(Schmidt-Nielsen et al., 1981)<br>(Yousef et al., 1989)             | Mask respirometry Mask respirometry Mask respirometry |
| Dromedary                           | 359                                     |     |                            |                   |               | (Farid et al., 1990)  | Intake & BM change                                    |
| Dromedary                           |   |     | 216                        | 203               |               | (Evans et al., 1994)  | Mask respirometry                                     |
| Dromedary                           | 374                                     |     |                            |                   |               | (Farid, 1995)   | Intake & BM change                                    |
| Dromedary                           | 304                                     |     |                            |                   | 213           | (Guerouali et al., 1995)  | Chamber respirometry & heat production                |
| Dromedary                           |   |     | 299                        |                   |               | (Maloiy et al., 2009)   | Mask respirometry                                     |





| Species        | MEm                | MR  | Standing<br>MR             | Resting<br>MR | Fasting<br>MR | Source   | Based on  |
|----------------|--------------------|-----|----------------------------|---------------|---------------|--|---|
|                |                    |     | kJ kg <sup>-0.75</sup> day | 7-1           |               | •  |   |
| SAC            | 305                |     |                            |               |               | (Van Saun, 2006; NRC, 2007)                                      | Literature data                                     |
| Alpaca         | 297                |     |                            |               |               | (Flores et al., 1989)  | Cited in: (López and Raggi, 1992; San Martín, 1996) |
| Alpaca         | 276                |     |                            |               |               | (Newman and Paterson, 1994)                                      | Intake & BM change                                  |
| Alpaca         | 440                |     |                            |               |               | (Russel and Redden, 1997)  | Intake & BM change                                  |
| Alpaca         |                    | 215 |                            | 144           |               | this study   | Chamber respirometry                                |
| 110000000      |                    |     |                            |               |               | (Schneider et al., 1974; Rübsamen                                |   |
| Llama          | 256                |     |                            |               | 218           | and von Engelhardt, 1975; von<br>Engelhardt and Schneider, 1977) | Intake & BM change, chamber respirometry            |
| Llama          |                    |     | 363                        |               |               | (El-Nouty et al., 1978)  | Mask respirometry                                   |
| Llama          |                    |     | 341                        |               |               | (Hochachka et al., 1987)   | Mask respirometry                                   |
| Llama          | 310-354            |     | 9.71                       |               | 248           | (Carmean et al., 1992)   | Chamber respirometry & heat production              |
| Llama          | 296-343            | 313 |                            |               | 2-10          | (Vernet et al., 1997)  | Chamber respirometry & heat production              |
| Llama          | (m) 10 m(1 m (2 m) | 290 |                            |               |               | (Nielsen et al., 2010)   | Chamber respirometry                                |
| Llama          |                    | 261 |                            | 164           |               | this study   | Chamber respirometry                                |
| Dromedary      |                    |     |                            | 215           |               | (Schmidt-Nielsen et al., 1967)                                   | Mask respirometry                                   |
| Dromedary      |                    |     |                            | 206           |               | (Schmidt-Nielsen et al., 1981)                                   | Mask respirometry                                   |
| Dromedary      |                    |     | 256                        | 230           |               | (Yousef et al., 1989)  | Mask respirometry                                   |
| Dromedary      | 359                |     |                            |               |               | (Farid et al., 1990)   | Intake & BM change                                  |
| Dromedary      |                    |     | 216                        | 203           |               | (Evans et al., 1994)   | Mask respirometry                                   |
| Dromedary      | 374                |     |                            |               |               | (Farid, 1995)  | Intake & BM change                                  |
| Dromedary      | 304                |     |                            |               | 213           | (Guerouali et al., 1995)   | Chamber respirometry & heat production              |
| Dromedary      |                    |     | 299                        |               |               | (Maloiy et al., 2009)  | Mask respirometry                                   |
| Bactrian camel |                    | 248 |                            | 192           |               | this study   | Chamber respirometry                                |



#### Conclusions

Both ad libitum intake and maintenance energy recommendations/ metabolism measurements support a lower metabolism in camelids as compared to domestic ruminants.

This could explain various observations incl. the competitive capacity of camelids in resource-poor environments.

Distinct variability in metabolism measurements could be an indicator of methodological issues or seasonality effects.

